# Dispersal Strategies of the Biota on an Oceanic Seamount: Implications for Ecology and Biogeography

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**Abstract.** Cobb Seamount lies at 46° 46′ N, 130° 48′ W in the northeast Pacific 510 km due west of the Oregon coast. The isolated seamount rises 3000 m in a current field flowing from west to east. The seamount supports dense populations of fish and benthos. Collections and submersible observations of the benthic community produced a list of 117 species representing 13 phyla. The organisms present can nearly all be found on the North American Pacific coast, but the diversity is low. This paper presents an analysis of the larval dispersal modes of the benthos at Cobb Seamount. This remote seamount is dominated by species with either a short-lived or no planktonic larval phase. The preponderance of such larval strategies and the observation of abundant drifting kelp near the seamount suggest that rafting of adults may be an effective dispersal mode. The presence of a recirculating flow in the form of a modified Taylor cap appears important for trapping short-lived larvae on the seamount. However, because the water mass is replaced about every 17 days, medium and long-lived larvae would not be retained. The interplay between local currents, available dispersal vectors, and life-history strategies cannot be overlooked in the interpretation of marine biogeographic patterns.

## Introduction

The study of marine biogeography requires an appreciation of the dispersal capabilities of component species at various stages in their life histories. Recognition of vicariant events can reveal large-scale patterns, but differential dispersal capabilities among species modify those patterns. Investigations of species accumulation on the marine equivalent of islands—seamounts—test our ideas about mechanisms of biogeographic patterning. Seamounts have been considered as stepping stones, vicariant pathways, and points of endemic isolation (Hubbs, 1959; Briggs, 1974; Wilson and Kaufmann, 1987; Leal and Bouchet, 1991).

Marine invertebrates show various development patterns ranging from metamorphosed juveniles emerging directly from broods through yolk-supported (lecithotrophic) floating larvae to plankton-feeding (planktotrophic) larvae (see reviews by Mileikovsky, 1971; Grahame and Branch, 1985; Scheltema, 1986b). In some clades, taxa are constrained to a single developmental mode (Woollacott and Zimmer, 1978; Nielson, 1980); in others, life history strategies vary within a given family (Hadfield and Strathmann, 1990), genus (Johannesson, 1988), or even species (Levin, 1984). Planktonic larvae are considered the primary dispersal mechanism for benthic marine invertebrates (Mileikovsky, 1971; Jackson, 1986). Longer planktonic duration should allow for greater dispersal of larvae (Zinsmeister and Emerson, 1979; Scheltema 1986a, b). Prevailing theory predicts that species with long-lived planktonic larvae will have broader geographic ranges, whereas those with short-lived or brooded larvae will be geographically restricted (Mileikovsky, 1971; Hedgecock, 1986; Scheltema, 1986b, 1989) but better able to capitalize on favorable local environments (Jackson, 1986; Keogh and Chernoff, 1987).

Johannesson (1988) suggested that isolated islands and seamounts are more likely to be populated by species with limited larval dispersal abilities on the basis that a founder population can achieve reproductive success. Some observations of species with limited larval range in isolated marine habitats support this idea (Birkeland, 1971; Moore, 1977; Johannesson, 1988).

Cobb Seamount presents the opportunity to examine concepts of larval dispersal capabilities and biogeography. It lies far enough offshore to provide a habitat disjunct from coastal communities but close enough that larvae could be expected to gain access with some regularity. The seamount (46° 46' N, 130° 47' W) is located in the northeast Pacific, 510 km due west of the Oregon (USA) coast (Fig. 1). Early surveys (Budinger and Enbysk, 1960; Budinger, 1967) described a symmetrical seamount with several terraces and a central pinnacle measuring about 800 by 600 m. Our surveys record a shallowest depth of 24 m. Cobb was formed near the Juan de Fuca Ridge as part of the Cobb-Eickelberg Seamount chain (Davis and Karsten, 1986). Summit lavas were eruptive during the Pleistocene; samples date to 1.6 ± 0.3 million years ago (Dymond et al., 1968). Farrow and Durant (1985) interpret submarine erosional features as stages in island subsidence and sea-level fluctuation. Beach characteristics are noted as deep as 310 m and may relate to the volcano's initial emergence. Low sea-level stands during the Wisconsin glacial period generated the large wave-cut terrace at 120–180 m.

Predominant flow is eastward at about 10 cm s$^{-1}$ in the North Pacific Current which, in the vicinity of Cobb, splits into the northward Alaska Current and the southward California Current (Hickey, 1989). Well-defined surface currents from the coast offshore do not exist. Surface drifters released near Cobb move linearly from northwest to southeast and do not reflect deeper eddying or circulation (Dower et al., 1992). A recent study documents the surface drift and flow around Cobb in more detail (Freeland, 1994). Early work by Birkeland (1971) reports dense assemblages of coastal species that include several brooders; many abundant inshore species are absent. In view of our diving experience on Cobb, we wondered how any population dependent on pelagic larvae could maintain itself: the open ocean surge is extreme and the persistent surface currents are likely to sweep propagules off the seamount.

Our study has three objectives: (1) to document the Cobb Seamount benthic community components, (2) to assess how these species may have arrived on the seamount, and (3) to examine the potential for development of stable populations in light of information from concurrent studies on the hydrodynamic processes around Cobb Seamount.

## Materials and Methods

We examined the Cobb benthos during several cruises as part of a larger effort to characterize the oceanographic conditions around the seamount. The submersible support vessel *Pandora II* visited twice in the early 1980s and the Canadian Survey Ships *Parizeau* and *J. P. Tully* partici-
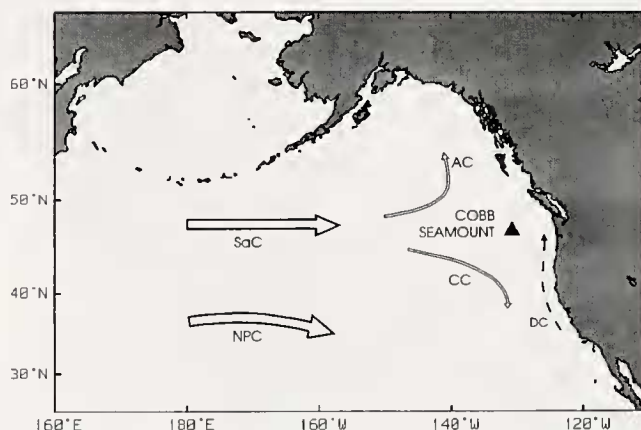


**Figure 1.** Location of Cobb Seamount in the northeast Pacific. Arrows indicate the major current patterns: SaC = Subarctic Current; AC = Alaska Current; NPC = North Pacific Current; CC = California Current; DC = the ephemeral Davidson Current.

pated in an oceanographic program in the summers from 1990 to 1992. The Canadian submersible *Pisces IV* conducted six dives in July 1982 and one dive in 1983; four of these dives covered parts of the terrace or pinnacle, and the other three were deeper. Collection was possible with the manipulator, which retrieved some voucher specimens. Most dive information came from still-camera photographs and diver records from which only organisms that were clearly identifiable were used. Dredging was attempted during surface cruises of 1990 and 1991, but the recovery was poor on the rock outcrops. Best returns from the pinnacle came from examination of the epifauna on detached rock scallops (*Crassadoma gigantea*). The pinnacle top was nearly impossible to sample because of the wave surge during diving and the lack of loose aggregates for dredging. Some algal and epifloral samples were retrieved on fishing lines. The most complete collection and identification information came from the benthic assemblage on the upper terrace and pinnacle. For that reason, we limit our presentation and analysis to species recorded above 180 m depth.

To identify invertebrates from the 1990 and 1991 samples we used Kozloff (1987), with reference to Bernard (1972), Lambert (1981, 1986), and Laubitz (1970) for the Brachiopoda, Echinodermata, and caprellid amphipods respectively. We used Hatch (1947) for the tanaids and isopods, and Gabrielson et al. (1989) for the algae. Local authorities helped us with many identifications. We added additional species documented in Birkeland (1971) and a list of fish species compiled by D. Nelson (unpub. data) to produce the final species listing.

The literature provided information on propagule dispersal periods of the seamount species. Although our efforts focused on individual species, assumptions were made for species within groups known to have invariant

dispersal modes. Species with crawl-away juveniles released from the adult or a benthic egg case form the "direct release" category. Species with pelagic larvae were categorized according to the length of time the larvae remain in the water column: less than 2 weeks = "short pelagic"; more than 2 but less than 8 weeks = "medium pelagic"; and more than 8 weeks = "long pelagic." Those species for which no information was available were left in an "unknown" category.

We constructed the expected distributions for larval dispersal modes of the benthic invertebrates from published information. Thorson (1961) presented the larval life spans of 195 species (no geographic range identified), which we redistributed in the time categories used in this paper. To add the category of nonpelagic development, we used the values of Thorson (1950) and Mileikovsky (1971); these numbers differ so we calculated the range of expected development types. Because many benthic invertebrates exhibit a latitudinal gradient in ratio of direct to pelagic developers (Thorson, 1950, 1961; Mileikovsky, 1971; Valentine and Jablonski, 1983), we used literature data only from Cobb's approximate latitude (38° N to 51° N). We restricted our final analysis to the benthic invertebrates because (1) a good body of theoretical and empirical work exists for comparison in this group, and (2) adult fish mobility may provide a source of migration unavailable to other organisms.

## Results

### The shallow Cobb community

The pinnacle top appears much as described by Birkeland (1971) who explored with scuba divers. The substratum is covered with coralline algae topped by patches of other algae (mostly *Desmarestia viridis*). Rock scallops (*Crassadoma gigantea*) with abundant epifauna inhabit cracks in the basalt. The sides of the pinnacle from 35 to 110 m support the densest aggregations of animals: little bare substratum is seen. A hummocky effect was created by the cementing scallops that are colonized by cnidarians (mostly *Corynactis californica*), tunicates, sponges, and bryozoans. Aggregations of the urchin *Strongylocentrotus franciscanus* are common at the shallower depths. Rockfish (*Sebastes* spp.) are very abundant in the water, with pelagic juveniles forming large schools.

The terrace at 125 to 300 m is mostly covered with white carbonate sediments through which some basalt outcrops protrude. Here echinoderms dominate the macrofauna. The crinoid *Florometra serratissima* and a variety of ophiuroids cover both sediments and outcrops. The asteroids *Pycnopodia helianthoides* and *Crossaster papposus* are common predators. Sediment samples recovered many gastropods and hermit crabs. Biomass on both pinnacle and terrace appears high. Comparison of the species list and photographs (from the University of Washington collection) of Birkeland (1971) with photographs and observations from 1982/83 and the samples of 1990/91 reveals little change in the composition of common and abundant species. There appear to have been outbreaks of the anenome *Metridium senile* and the sea urchin *Strongylocentrotus franciscanus,* but the overall species composition seems stable.

Table 1 lists the species known to occur at Cobb Seamount above 180 m. In total, 117 species from 13 phyla have been identified to date. Several species of nematodes, protozoa, and polychaetes remain unidentified and are not included. The fauna is depauperate compared to the coastal communities of the northeast Pacific. For example, a count of the benthic invertebrates (0 to 250 m) in a preliminary list of animals from the west coast of Vancouver Island (Austin, 1970) reaches 786 using only the phyla found on Cobb, where the equivalent number is 95.

### Methods of propagule dispersal

For 26 of the 117 Cobb species (22.2%), dispersal data are unavailable or cannot be inferred; 26.5% release their juveniles directly onto the substratum; and 37.6% have propagules in the short pelagic category. Although this category includes species whose larvae spend up to 2 weeks in the plankton, the larvae of most of the species remain pelagic for a few days to just minutes. Species belonging to the medium and long pelagic larval dispersal groups each make up 6.8% of all Cobb species.

Figure 2A illustrates the distribution of propagule dispersal types recorded for the benthic invertebrates of Cobb Seamount. Among the 95 species, 31.6% are direct releasers and 32.6% belong to the short pelagic group. Medium and long pelagic larval dispersal groups make up 8.4% and 4.2% of all species respectively. Larval dispersal methods of 25.3% of Cobb invertebrate species remain unknown. Of the 12 species we classified as abundant (Table I), 8 have no planktonic larval phase, 2 are short pelagic, and 2 are long pelagic; no abundant species have a medium-length pelagic larval dispersal phase.

The calculated expected distribution of larval dispersal types for benthic marine invertebrates at the approximate latitude of Cobb Seamount is presented in Figure 2B. The ranges of values observed for this latitude are as follows: direct release, 26.0–36.5%; short pelagic, 9.5–11.1%; medium pelagic, 45.1–52.5%; long pelagic, 8.9–10.4%. No comparable "expected" data set exists for the Pacific northwest. We searched for information on polychaete reproduction from Strathmann (1987) and references therein because this group shows the whole range of reproductive strategies. For 46 coastal species, division of larval lifetimes were 13 direct, 8 short, 23 medium, and 2 long pelagic.

**Table I**

*Systematic listing of species known to occur on Cobb Seamount, indicating relative abundance (for those identified from 1990 and 1991 collections), dispersal method, source of species identification, and references concerning dispersal method*

| Phylum | Class | Species | Abundance[†] | Dispersal Mode[‡] | Source of ID[§] | Reference[‖] |
|---|---|---|---|---|---|---|
| Chlorophyta | Ulvophyceae | *Pseudopringsheimia apiculata* | ? | short pelagic* | B | (30) |
| Phaeophyta | Phaeophyceae | *Desmarestia viridis* | A | short pelagic* | C | (30) |
| | | *Ectocarpus corticulatus?* | C | short pelagic* | C | (30) |
| Rhodophyta | Rhodophyceae | *Antithamnion kylnii* | C | short pelagic* | C | (30) |
| | | *Mastocarpus jardinii?* | R | short pelagic* | C | (30) |
| | | *Polysiphonia pacifica* | R | short pelagic* | C | (30) |
| | | *Polysiphonia urceolata* | C | short pelagic* | C | (30) |
| | | *Ceramium* sp. | R | short pelagic* | C | (30) |
| | | *Lithothamnion* sp. | A | short pelagic* | O/B | (30) |
| | | *Lithophyllum* sp. | ? | short pelagic* | B | (30) |
| | | *Delesseria* sp. | R | short pelagic* | C | (30) |
| | | *Porphyropsis* sp. | R | short pelagic* | C | (30) |
| | | unk. red blade | R | short pelagic* | C | (30) |
| Porifera | Desmospongiae | *Halichondria panicea* | C | short pelagic | W | (1) |
| Cnidaria | Hydrozoa | *Allopora verrilli* | A | direct release* | P/W | (23, 36) |
| | Anthozoa | *Desmophyllum cristigalli* | C | unknown | W | |
| | | *Cribrinopsis fernaldi* | ? | short pelagic | P/B | (34) |
| | | *Metridium senile* | C | short pelagic | P | (3, 15, 23) |
| | | *Corynactis californica* | A | direct release | P/C | (23) |
| | | *Urticina crassicornis* | ? | short pelagic | P | (4) |
| | | *Stomphia didemon* | ? | short pelagic | P | (33) |
| | | *Stylatula elongata* | ? | short pelagic | P | (23) |
| | | *Epizoanthus?* sp. | ? | unknown | P | |
| | | colonial zoanthid? | R | unknown | C | |
| Annelida | Polychaeta | *Crucigera zygophora* | C | medium pelagic | C | (20, 36) |
| | | *Nothria conchylega* | R | direct release | C | (31) |
| | | *Phyllochaetopterus prolifica* | A | direct release | C | (23) |
| | | *Protula pacifica* | R | short pelagic | C | (20) |
| | | *Phyllodoce maculata* | ? | medium pelagic | B | |
| | | *Trypanosyllis gemmipara* | ? | unknown | B | |
| | | *Nereis procera* | ? | short pelagic | B | (36) |
| | | *Eunice valens* (=*E. kobiensis*) | ? | direct release | B | (36) |
| | | *Serpula vermicularis* | ? | short pelagic | B | (23) |
| | | *Chitinopoma groenlandica* | ? | unknown | B | |
| | | *Euphrosine* sp. | R | unknown | C | |
| | | *Lumbrineris inflata* | A | short pelagic | C | (20, 36) |
| | | cirratulid sp. 1 | C | short pelagic* | C | (23, 36) |
| | | spirorbid sp. 1 | A | short pelagic* | C | (27) |
| | | trichobranchid(?) sp. 1 | R | unknown | C | |
| | Oligochaeta | oligochaete sp. 1 | C | direct release | C | |
| Arthropoda | Amphipoda | *Caprella alaskana* | A | direct release* | C | (23) |
| | | *Caprella laeviuscula* | C | direct release* | C | (23) |
| | | gammaridean sp. 1 | C | direct release* | C | (23, 25, 40) |
| | | *Proboloides?* n. sp. | C | direct release* | C | (23, 25, 40) |
| | | *Micropleustes* n. sp. | A | direct release* | C | (23, 25, 40) |
| | | gammaridean sp. 4 | C | direct release* | C | (23, 25, 40) |
| | | *Parapleustes* n. sp. | A | direct release* | C | (23, 25, 40) |
| | | gammaridean sp. 6 | A | direct release* | C | (23, 25, 40) |
| | | gammaridean sp. 7 | R | direct release* | C | (23, 25, 40) |
| | | *Maera* n. sp. | R | direct release* | C | (23, 25, 40) |
| | Copepoda | calanoid copepod | R | unknown | C | |
| | | cyclopoid copepod | R | unknown | C | |
| | | harpacticoid copepod | C | short pelagic* | C | (13) |
| | Isopoda | *Ianiropsis tridens* | C | direct release* | C | (23) |
| | | *Munna ubiquita* | C | direct release* | C | (23) |
| | | *Munna chromatocephala* | C | direct release* | C | (23) |

**Table 1** *(continued)*

| Phylum | Class | Species | Abundance[†] | Dispersal Mode[‡] | Source of ID[§] | Reference[‖] |
|---|---|---|---|---|---|---|
| Arthropoda | Tanaidacaea | *Leptochelia* sp. | C | direct release* | C | (23) |
| | | *Paratanais* sp. | C | direct release* | C | (23) |
| | Malacostraca | *Chorilia longipes* | C | medium pelagic* | C | (14) |
| | | *Oregonia gracilis* | C | medium pelagic* | C | (14) |
| | | *Pagurus cavimanus* | ? | unknown | B | |
| Mollusca | Gastropoda | *Acmea instabilis* | R | unknown | W | |
| | | *Margarites marginatus* | C | direct release | W | (36) |
| | | *Calliostoma annulatum* | R | short pelagic | W | (10, 36) |
| | | *Calliostoma ligatum* | C | short pelagic | C/W | (16) |
| | | *Homalopoma carpenteri* | R | unknown | W | |
| | | *Diodora aspera* | R | direct release | C | (39) |
| | | *Searlisia dira* | C | direct release | W | (23) |
| | | *Ocenebra lurida* | ? | direct release | B | (8) |
| | | *Fusitriton oregonensis* | ? | unknown | B/O/C | |
| | | *Granulina margaritula* | C | direct release | C | (26) |
| | | *Barleeia/Cingula* | ? | unknown | W | |
| | | *Bittium* sp. | ? | unknown | W | |
| | | *Battilaria/Antiplanes* | ? | unknown | W | |
| | | *Diorina albolineata* | ? | unknown | B | |
| | | *Archidoris montereyensis* | ? | short pelagic | B | (23) |
| | | *Archidoris odhneri* | ? | unknown | B | |
| | Bivalvia | *Crassodoma gigantea* | A | long pelagic | P/C | (23) |
| | | *Macoma balthica* | R | medium pelagic | W | (6) |
| | | *Modiolus modiolus* | R | medium pelagic | C | (5) |
| | | *Petricola pholadiformis* | R | medium pelagic | C | (18) |
| | | hiatellid sp. | R | long pelagic | C | (23) |
| | | philobryid sp. | R | unknown | C | |
| | | solemyid sp. | R | short pelagic* | C | (9) |
| Brachiopoda | Articulata | *Laqueus californianus* | ? | short pelagic* | O/W/P | (37) |
| | | *Terebratulina* sp. | ? | short pelagic* | O/P | (37) |
| | | *Platidia hornii* | C | short pelagic* | C | (29) |
| Bryozoa | Cyclostomata | *Bicrisia edwardsiana* | C | short pelagic* | C | (24, 41) |
| | | *Crisia occidentalis* | C | short pelagic* | C | (24, 41) |
| | | *Filicrisia franciscana* | C | short pelagic* | C | (24, 41) |
| | Cheilostomata | *Rhamphostomella spinigera* | ? | short pelagic* | B | (41) |
| | | *Borgiola pustulosa* | ? | short pelagic* | B | (41) |
| | | *Bugula* sp. | C | short pelagic* | C | (24, 41, 42) |
| | | *Lyrula* sp. | C | short pelagic* | C | (41) |
| Sipuncula | | *Phascolosoma agassizi* | C | short pelagic | C | (28, 36) |
| Echinodermata | Asteroidea | *Pycnopodia helianthiodes* | C | long pelagic | P | (7, 17, 23, 35) |
| | | *Crossaster papposus* | C | medium pelagic | C/P | (17, 36) |
| | | *Henricia sanguinolenta* | R | direct release | C | (17, 23, 32) |
| | | *Henricia leviuscula* | C | direct release | C | (17, 23) |
| | | *Orthasterias koehleri* | ? | unknown | B | |
| | | *Leptasterias hexactis* | R | direct release | C | (17, 23) |
| | | *Solaster* sp. | ? | unknown | O/P | |
| | | *Hippasterias spinosa* | ? | short pelagic | O | (17) |
| | Ophiuroidea | *Amphipholis squamata* | ? | direct release | B | (38) |
| | Crinoidea | *Florometra serratissima* | A | short pelagic | P | (19, 22, 35) |
| | Echinoidea | *Strongylocentrotus franciscanus* | A | long pelagic | C | (23, 35, 36) |
| | Holothuroidea | *Parastichopus leukothele* | R | unknown | W | |

**Table I** *(continued)*

| Phylum | Class | Species | Abundance[†] | Dispersal Mode[‡] | Source of ID[§] | Reference[‖] |
|---|---|---|---|---|---|---|
| Chordata | Ascidiacea | *Ascidia ceratodes* | ? | short pelagic* | P | (21) |
| | Chondricthyes | *Prionace glauca* | ? | direct release | B | (12) |
| | Osteichyes | cottid fish | R | unknown | C | |
| | | *Sebastes helvomaculatus* | A | long pelagic | N | (2) |
| | | *Sebastes paucispinus* | A | long pelagic | B/N | (2) |
| | | *Sebastes entomelas* | A | long pelagic | B/N | (2) |
| | | *Sebastes ruberrimus* | A | long pelagic | B/N | (2) |
| | | *Hemilepidotus spinosus* | A | unknown | B/N | |
| | | *Embassichthys bathybius* | C | unknown | N | |
| | | *Mola mola* | ? | unknown | B | |

[†] Abundance Categories: A = abundant: two or more samples with several individuals; C = common: several individuals in one sample or two or more samples with at least 1 individual; R = rare: one or two individuals in only one sample; ? = abundance not estimated due to data source.

[‡] Dispersal Categories: Direct release: budding, fission, or benthic juveniles emerging from parent or benthic egg case; short pelagic: short-lived (<2 weeks) planktonic larvae, usually lecithotrophic; medium pelagic: usually planktotrophic larvae with a 2–8 week residence in the plankton; long pelagic: planktotrophic larvae with >8 week residence in the plankton.

[§] Source of species list: B = from Birkeland (1971); C = identified from collections made in 1990–1992; N = from an unpublished list compiled by Douglas Nelson (1983); O = from *Pisces* observations in early 1980s; P = identified from *Pisces* photographs; W = identified from our collection by W. C. Austin.

[‖] References: (1) Amano, 1986; (2) Boehlert & Yoklavich, 1984; (3) Chia, 1976; (4) Chia & Spaulding, 1972; (5) deSchweinitz & Lutz, 1976; (6) Gilbert, 1978; (7) Greer, 1962; (8) Griffith, 1967; (9) Gustafson, 1985; (10) Hadfield & Strathmann, 1990; (11) Hart, 1960; (12) Hart, 1973; (13) Hicks & Coull, 1983; (14) Hines, 1986; (15) Hoffmann, 1987; (16) Holyoak, 1988; (17) Lambert, 1981; (18) Mackie, 1984; (19) McEdward *et al.,* 1988; (20) D. McHugh, pers. comm.; (21) Millar, 1971; (22) Mladenov & Chia, 1983; (23) Morris *et al.,* 1980; (24) Nielsen, 1970; (25) Nielson, 1980; (26) T. Parker, pers. obs.; (27) Potswald, 1978; (28) Rice, 1967; (29) Rudwick, 1970; (30) Santelices, 1990; (31) Schroeder & Heimans, 1975; (32) Shield & Witman, 1993; (33) Seibert, 1973; (34) Seibert & Spaulding, 1976; (35) Strathmann, 1978; (36) Strathmann, 1987; (37) Valentine & Jablonski, 1983; (38) Walker & Lesser, 1989; (39) Webber, 1977; (40) Wildish, 1982; (41) Woollacott & Zimmer, 1978; (42) Woollacott *et al.,* 1989.

* Larval dispersal mode inferred from related species within groups showing a phylogenetic constraint on larval dispersal modes.

## Discussion

Many authors emphasize the importance of larvae as dispersal mechanisms for marine invertebrates (*e.g.,* Zinsmeister and Emerson, 1979; Valentine and Jablonski, 1983; Scheltema, 1986a, b). "Good dispersers" dominate the molluscan faunas of oceanic islands (Scheltema and Williams, 1983). In this context, species with longer larval stages should dominate the Cobb benthos. What we find, conversely, is a poor representation by such species, suggesting that enhanced larval dispersability contributes little to population establishment or maintenance on this seamount. In fact, it appears that long-lived larvae may be a distinct disadvantage: only 15 of the 89 species for which we have good information had larvae pelagic for more than 2 weeks. Comparison with the expected proportion from equivalent latitudes (Fig. 2 and polychaete comparison data) underscores the depletion of these groups. The paucity of species with a medium-duration planktonic larval phase is quite intriguing. This group, which otherwise represents the largest proportion of species at this latitude, includes many species conspicuously absent from Cobb.

The proportion of species with direct development, while similar to the general observations for the latitude, is surprising on an isolated seamount. A study of gastro-pods on a series of Brazilian seamounts finds direct developers averaging only 7% of the fauna on each seamount (Leal and Bouchet, 1991). One can argue that once a founder group of such a species somehow arrives, it is liable to establish a population by self-recruitment. However, the large number of species with larvae pelagic for even less than 2 weeks still seems anomalous; on Cobb Seamount, tidal currents, surface currents at 10 cm s$^{-1}$ (Freeland, 1994), and storm surges appear sufficient to sweep water-borne larvae far from a shallow substratum.

From the point of view of vicariance biogeography, species accumulation may represent relict distributions. Cobb Seamount was an emergent island during the last glaciation. While the coast south to 48° N was engulfed in an ice-sheet, Cobb represented an offshore refuge. That this island was colonized at this time is known. Sub-fossil debris of intertidal organisms such as bivalves and barnacles litters the 120-m terrace. Budinger (1967) dated one mussel shell at 6710 ± 330 years before present. This *Mytilus* species is no longer extant on the seamount because rising sea levels drowned the intertidal zone. We cannot know which of the remaining species have maintained populations since that time. Between Cobb Seamount and the coast lie a bare rock spreading ridge and a bathyal plain that form barriers to both vicariant path-
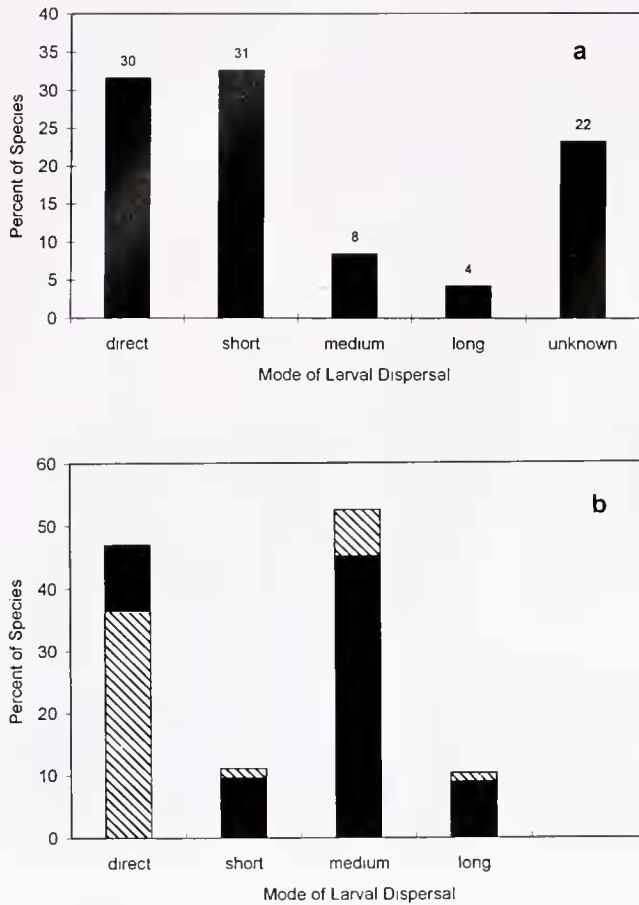
**Figure 2.** (a) Distribution of larval development modes for the invertebrate species of Cobb Seamount. This presentation represents 95 invertebrate species. Details are given in Table I. Direct = species that have no pelagic stage; short = species with larvae pelagic for 2 weeks or less; medium = species with larvae that spend 2 to 8 weeks in the plankton; long = species with larvae that are pelagic for longer than 8 weeks. Above the columns are the numbers of invertebrates included. (b) Expected distributions of larval development modes for benthic invertebrates around the latitude of Cobb Seamount; values generated from Thorson (1950, 1961) and Mileikovsky (1961) as explained in the text. Because these authors give different values for the proportion of species that are direct releasers, we present a distribution with a maximum value for direct release (black) and one using a minimum value (pattern).

ways and individual adult migration. The nearest seamounts have summits below 500 m; only Union Seamount, 370 km north-north-west, is shallower.

We believe present dispersal does play a major role. All but four undescribed amphipod species are found on the North American coast; several have wider distributions. The seamount sits at the divergence of an eastward flow field; flow further east splits into the Alaskan and California Currents. Two seasonal currents, shallow Davidson and deep California Undercurrent, flow poleward from California hugging the coast (Hickey, 1989). Stray jets may extend offshore occasionally, but even a 15 cm s⁻¹

current will take some 6 weeks to carry a larva from the coast. Medium- and short-duration larvae from surrounding continents are unlikely to survive the trip to Cobb. There are no other shallow seamounts nearby. The Alaskan gyre could bring long-lived larvae over thousands of kilometers from Alaska. Species with larvae of long planktonic duration may arrive from Alaska, the Pacific Northwest, California, or even Japan. The rock scallop *Crassadoma gigantea* was examined by protein electrophoresis for evidence of population differentiation between Cobb and British Columbia. Allozyme frequencies of several loci revealed no significant differences diagnostic of isolated populations (Dower and Tunnicliffe, unpub. data). This scallop releases pelagic larvae that are viable for several weeks. It is also noteworthy that, of the eight species with long pelagic dispersal, all but one have long adult lifespans (20 years or longer). Such populations have the potential to survive between infrequent recruitment events.

Johannesson (1988) predicts the result that we present: a paucity of species with longer pelagic larvae on Cobb Seamount. He proposes that successful colonization of isolated areas is enhanced by limited off-site advection of the founder population's progeny. His model emphasizes the role of dispersal agents in medium latitude oceans. He states, in fact, that presence of a species with a longer-lived larva on a place like Cobb Seamount is more problematic than that of a direct-developer.

Kelp is often observed floating near and over Cobb Seamount, although these macroalgae do not grow there. The large kelp forests of the west coast of North America support a rich, dense fauna. Because of considerable hydrodynamic drag, large kelps often break free (Koehl and Wainwright, 1977) and the associated epiphytic species may linger for over 100 days (Vàsquez, 1993). Floating kelp rafts move with the surface winds rather than with prevailing current; they can travel at averaged speeds of 5 to 10 cm s⁻¹ and instantaneous speeds to 65 cm s⁻¹ (Harrold and Lisin, 1989). Winds from the southwest could carry kelp from the California coast during the winter domination of the Aleutian low-pressure cell. Kelp rafts may provide a significant migration vector for metamorphosed invertebrates regardless of their larval development mode (Knox, 1954; Highsmith, 1985; Johannesson, 1988; Lane *et al.*, 1985; Sörlin, 1988; O'Foighil, 1989; Martel and Chia, 1991). Most epifaunal species listed in Table I can be found in kelp forests. Several, such as *Strongylocentrotus franciscanus, Acmaea instabilis,* and the *Calliostoma* species, are rarely found elsewhere. Given that rafts can deliver juveniles and adults to an isolated site, those species with brooded and short-lived larvae may be superior colonizers through subsequent local recruitment (Jackson, 1986; Keough and Chernoff, 1987) and adaptation (Behrens Yamada, 1989). In some cases, spe-

cies with short or no planktonic larval periods have wider geographic ranges than those with longer larval periods (Levin, 1984; Johannesson, 1988; O'Foighil, 1989).

In both the early and late 1980s, we collected many of the species recorded by Birkeland (1971) in the 1960s. Persistent populations must propagate locally or have a constant recruitment. Direct-release species have little opportunity to spread further. Although we have not examined genetic characteristics in such species, population differentiation is demonstrated for two species of brooding crustaceans on two other isolated seamounts (Bucklin et al., 1987; Wilson and Boehlert, 1993). Four of our direct-release amphipod species are new species or subspecies (Bousefield, pers. comm.). This feature argues for the persistence of isolated populations on Cobb Seamount.

A look at the local flow regime helps to explain the preponderance of species with larvae that are pelagic for 2 weeks or less. Dispersal in species with short-lived larvae is affected by water-flow patterns in a highly deterministic fashion (Olson, 1985; Bingham, 1992). Freeland (1994) has demonstrated the presence of a circulating flow around Cobb Seamount. He models the conditions necessary for formation of a "Taylor Proudman column" caused by the displacement of a stratified, linear current flow in the presence of the seamount (Hogg, 1973; Chapman and Haidvogel, 1992). Freeland (1994) describes anticyclonic flow around Cobb that is strongest near the base of the water column; it extends about 100 m upwards but does not penetrate to the surface. The lowest current meters identify an outflow in the bottom Ekman layer. Freeland estimates that the circulating water is replaced over about 17 days and forms a steady concentric inflow that would effectively trap larvae. He concludes that the recirculation is due primarily to a Taylor Proudman cap. Concentration of plankton over such topographic features has been recorded (Boden, 1952; Genin and Boehlert, 1985) and a recirculation mechanism implicated (Pingree and Maddock, 1985; Boehlert, 1988; Dower et al., 1992). There is, therefore, a mechanism to retain larvae in our "short-lived" group near the seamount until resettlement and metamorphosis on the seamount can occur.

Recruitment to Cobb of many common species from the North American west coast is limited by their intermediate pelagic life span of 2 to 8 weeks. Fortuitous flow events such as eddies and jets that break away from the longshore flow (Hickey, 1989) may provide an occasional transport vehicle toward Cobb. Regardless of their means of arrival, populations established this way are liable to lose their own progeny as a result of the short residence time of water over their new domicile.

We found that classic theories of larval development strategy did not help us to predict the types of species that would accumulate on Cobb Seamount. Johannesson (1988), among others, questions the generality of the rel-

ative effectiveness of long-lived pelagic larvae as dispersal agents; our observations support his model. Species with long pelagic larval periods appear able to establish populations only if the species are long-lived as adults or the current supplying the larvae is consistent; there were few such species on Cobb. Most studies on teleplanic larvae are based in tropical/subtropical latitudes (Scheltema, 1971, 1986b; Zinsmeister and Emerson, 1979) where direct development and short-lived pelagic larvae are uncommon. In our case, the role of local flow around Cobb Seamount is likely the leading factor determining the success of species with different larval strategies. Although we have no direct evidence, the role of rafting deserves serious consideration. In considering biogeographic and life-history theories, the marine biologist is well served by an understanding of the regional history, physical dynamics, and biological characteristics of the system under study.

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